

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON.

SOME INTERRELATIONS OF PLANTS AND INSECTS.*

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It is my purpose to-night to present some phases of the curious interrelations between plants and insects. In doing this I shall not have time to deal with the remarkable series of results that have followed the more careful and accurate investigation of the so-called insectivorous or carnivorous plants, and which have shown that these plants are not only possessed of the power of movement depending upon nerve stimuli, that may be likened in almost every respect to the automatic movements of animals, but that they actually possess digestive powers and properties which, chemically and functionally, are the same as those by which animals digest their food. It is my desire rather to call your attention to certain phases of plant fertilization by insects.

*This communication was presented for the most part extemporaneously, with the aid of stereopticon views. In preparing it, by request, for the printer, I have assumed that the facts already published in reference to *Yucca* pollination are familiar to the members of the Society, and have presented in the briefest manner such only as throw light on the philosophical portion of the article. The descriptive portion is condensed from a more extended paper recently prepared for the Annual Report of the Missouri Botanical Garden, but not yet published, and the illustrations are for the most part borrowed in advance from that paper. Figures 8, 10, 11, 12, and 13, however, are from my previous publications; Figure 6 was prepared specially from the stereopticon slide; and Figures 2, 3, and 4 are from the Department of Agriculture and used by permission of Assistant Secretary Willits.

I need not tell the members of this Society that the old idea that flowers were endowed with beauty and fragrance for our particular pleasure has been effectually set aside, and that these attributes have come to be looked upon in their true light, as essential to the plant's existence and perpetuation; that, in other words, color, form, odor, secretions, and the general structure of flowers, all have reference to insects. Nor need I dilate on the need of cross-fertilization in plants generally, or the modification which insect pollinizers have undergone as a consequence of this need. Some of the more interesting facts are particularly well exemplified in our orchids, to the philosophic study of which Darwin's important work "On the Fertilization of Orchids" gave a distinct impulse. But here we have adaptation of the plant only, and, with scarcely an exception, most flowers, including those of our orchids, may be fertilized by different insects. There are, in fact, few which are dependent on a single species for pollination, and, so far as I know, our *Yuccas* furnish the only instance of this kind. It is to the fertilization of these plants that I would first draw your attention.

The *Yuccas* are a characteristic American group of liliaceous plants, finding their home more particularly in the southern United States and Mexico. There are many species which have been divided even into sub-genera by Dr. Engelmann, as *Sarcococca*, *Clistoyucca*, *Chenoyucca*, and *Hesperoyucca*; but for our present purpose they may all be included under the one genus *Yucca*, as they all possess certain characteristics in common, viz, a thick, sub-mucilaginous root, which is in reality a subterranean stem; lance-shaped, evergreen leaves, narrow or broad, rigid or flaccid, and with the edges either filamentose, smooth, or more or less distinctly serrate. The leaves produce a coarse fiber, valuable for certain kinds of fabrics, while the trunks of the tree *Yuccas* have been used to make the toughest kind of paper. The fruit of some species, as of *aloifolia* and *baccata*, is fleshy and edible. It is, however, the flowers to which I would draw more especial attention. They are produced in large panicles, and are characterized as a rule by the anthers not reaching anywhere near the stigma; so that fertilization unaided can take place only by the merest accident. The *Yuccas* show great variation in detail, both in leaf, general habitus, flower-stalk, flower, and fruit, from the common sessile *Yucca filamentosa* of our gardens to the arboreal forms, like

brevifolia of the Mohave Desert and *filifera* of Mexico. My remarks will be based chiefly on *Yucca filamentosa*, which is indigenous to the Southeastern States and is cultivated beyond its natural range, under a number of horticultural variety names, in our gardens.

An examination of the flower will show at once the peculiarities which I have alluded to as characteristic of the genus. The stamens or filaments are bent away from the stigma and do not reach more than two-thirds the length of the pistil, the stigmatic opening being at the tip of the prolonged style and nowhere within reach of the stamens, while the pollen either remains attached to the open and withered anthers or falls in different sized lumps on the underside of the perianth. It cannot be introduced into the stigmatic tube without artificial aid, and the plant depends absolutely on the little white moth belonging to the Tineina and known as *Pronuba yuccasella* Riley.

STRUCTURAL CHARACTERISTICS OF PRONUBA.

Upon a superficial view, this little moth shows nothing very peculiar. The general coloration is white, the primaries being purely white on the upper surface; so that when at rest in the half open flowers of the *Yucca* it is not easily detected. The under surfaces, however, are dusky and offset in flight the whiteness of the rest of the body, so as to render the species somewhat difficult of detection while flitting from plant to plant. The male shows no very marked peculiarities to distinguish him from the other members of the family, the most noticeable being, perhaps, the prominence of the exposed parts of the genitalia. The female, however, shows some remarkable structural peculiarities, which admirably adapt her for the functions she has to perform, for she must fertilize the plant, since her larvæ feed upon its seeds.

Now, if I should ask any well-informed entomologist what are the characteristics of the Lepidopterous mouth, in the imago state, he would unhesitatingly answer: The lack of all prehensile organs and a coiled tongue capable of sucking liquids. If again I should ask what distinguishes the Lepidoptera from, say, the Hymenoptera, in the methods of oviposition, he would answer that the Lepidoptera lay eggs possessing, it is true, an infinite diversity of form, but usually attached externally to some part of the food-plant of the species, while the Hymenop-

tera as a rule secrete theirs, and are furnished with either a puncturing, boring, or sawing instrument for that purpose. The generalization would be entirely justified, though there are many curious exceptions to it, especially in the very group Tineina, to which our *Yucca* moth belongs. It is, however, necessary to

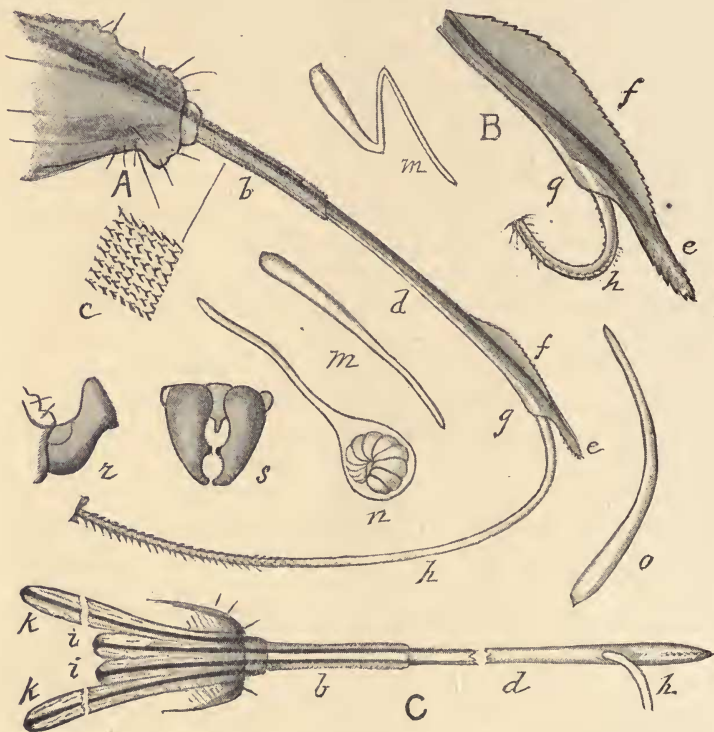


FIG. 1.—A, tip of anal joint and vaginal projection of ♀ *Pronuba yucca-ella* from side, showing ovipositor with parts extended; b, basal joint; c, its file-like surface; d, terminal joint, with its dorsal serrate wing (f), its dentate tip (e), its ventral membranous outlet (g), and the extended oviduct (h); B, the same parts further enlarged; C, ventral view of tip of abdomen, showing the two pair of rods *i, i* and *k, k*, with their muscular attachments, the parts of the ovipositor similarly lettered as in A; *m, m*, eggs taken from *Yucca* pistil; *n*, egg, showing development of embryo; *o*, mature egg from ovary of ♀; *r, s*, genital claspers of ♂, lateral and dorsal view—all enlarged.

state these general truths in order to convey a just idea of the exceptional nature of the two organs to which I wish more particularly to draw your attention. The first is a pair of maxillary tentacles which are prehensile and spinous on their under surface. They are peculiar to the genus *Pronuba* and exist in no other genus

of the many thousands of butterflies and moths.* The other organ is the ovipositor, which, instead of being a simple opening, as typically found in Lepidoptera, is here modified into a complex combination of lance and saw. Ordinarily it is withdrawn and hidden, but when in action is projected far beyond the tip of the abdomen and is then seen to consist of two principal parts the basal part being imbricato-granulate—*i. e.*, having a delicate file-like structure, the terminal part being smooth, but having near the end a dorsal serrate chitinous wing and a still more strongly toothed corneous tip. The internal structure is seen to consist of two stout rods, extending along the thin walls to the very tip, and of a ventral canal or passage-way for the delicate oviduct, which is silk-like and elastic and may be extruded for a great length from an outlet near the end of the ovipositor. This oviduct is smooth basally, but armed along its terminal third with retrorse hairs, increasing somewhat in number and strength toward the tip, around which they are almost spinous. At first sight these would seem to be out of place and to impede rather than aid the insertion of such a delicate filament; but, as we shall presently see, the act of oviposition is a most intricate and difficult one and these hairs are doubtless sensitive and tactile and serve the double purpose of enabling the moth to feel her way in the ovarian cell and of temporarily anchoring in the soft wall thereof while the egg is being passed to its destination. It will be seen that this ovipositor is admirably adapted for cleaving through the young fruit and then running the egg into the ovarian cavity, as will be presently described. The manner in which this ovipositor is worked by the four rods attached to strong muscles is indicated at Fig. 1, C, the two inner rods forming, as already indicated, the rigid portion of the ovipositor proper and the imbricate basal portion of the covering facilitating the invagination of the basal part when the ovipositor is withdrawn. The two outer rods are attached to strong muscular tissue in the walls of the vagina, and when the ovipositor is extended to its utmost limit this vaginal portion is partially extruded so as to appear like a basal subjoint. More detailed characterization of these parts is unnecessary in this connection.

* There are over 12,000 described species of Lepidoptera from Europe and America, and those from other parts of the world will double this number. Nearly as many more remain, perhaps, to be described.

THE ACTS OF POLLINATION AND OVIPOSITION.

Having thus drawn attention to the most characteristic structures of *Pronuba*, we shall better understand the following account of the acts of pollination and oviposition which I quote from an article recently prepared for the Annual Report of the Missouri Botanic Garden:

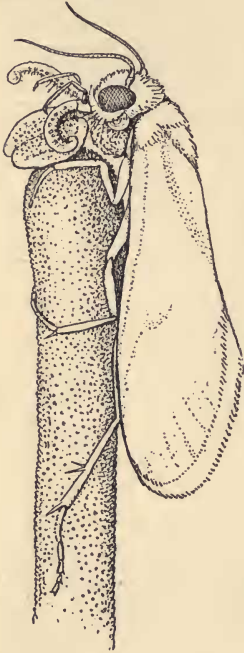


FIG. 2. — Female *Pronuba yuccasella* gathering pollen, $\times 5$.

“Though all the acts of the female are nocturnal, it is not at all difficult to follow them with a lantern, for, albeit ordinarily shy, she may be closely approached when about to oviposit. Her activity begins soon after dark, but consists, at first, in assiduously collecting a load of pollen. She may be seen running up to the top of one of the stamens and bending her head down over the anther, stretching the maxillary tentacles, so wonderfully modified for the purpose, to their fullest extent, the tongue uncoiled and reaching to the opposite side of the stamen. In this manner she is able to obtain a firm hold of the stamen, while the head is kept close to the anther and moved peculiarly back and forth, something as in the motion of the head of a caterpillar when feeding. The maxillary palpi are used in this act very much as the ordinary mandibles are used in other insects, removing or scraping the pollen from the anthers toward the tentacles. After thus gathering the pollen she raises her head and commences to shape it into a little mass or pellet by using her front legs very much as a cat does when cleansing her mouth, sometimes using only one leg, at another time both, smoothing and pressing the gathered pollen, the tentacles meanwhile stretching and curving. After collecting all the pollen from one anther she proceeds to another and repeats the operation, then to a third and fourth, after which, with her relatively large load—often thrice as large as the head—held firmly against the neck and front trochanters, she usually runs about or flies to another plant; for I have often noticed that oviposition, as a

rule, is accomplished in some other flower than that from which the pollen was gathered, and that cross-fertilization is thus secured.

"Once fully equipped with this important commodity, she may be seen either crawling over or resting within the flower, generally with the head toward the base. From time to time she makes a sudden dart and deftly runs around the stamens, and anon takes a position with the body between and the legs straddling two of them, her head being usually turned toward the stigma. As the terminal portion of the stamens is always more or less recurved, she generally has to retreat between two of them until the tip of her abdomen can reach the pistil. As

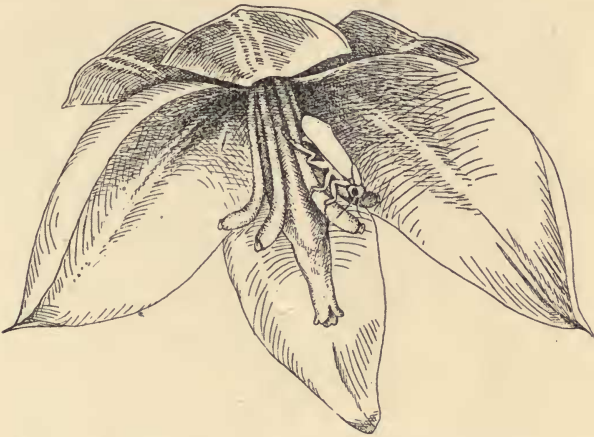


FIG. 3.—Flower of *Yucca filamentosa* with near petals removed, showing *Pronuba* in act of ovipositing.

soon as a favorable point is reached, generally just below the middle, she rests motionless for a short time, when the abdomen is slightly raised and the lance-like ovipositor is thrust into the soft tissue, held there the best part of a minute, while the egg is conducted to its destination, and then withdrawn by a series of up-and-down motions.

"In non-technical language, the pistil or the young fruit, below the stigmatic tube, shows externally at this time six quite distinct longitudinal divisions, each having a median ridge, there being six corresponding depressions or concavities in which the six stamens fit, especially at the base. Technically, the pistil is a three-celled ovary, the styles bifid at tip and united so as to

form the stigmatic tube. A transverse section anywhere about the middle will show that each of the six longitudinal sections contains a row of ovules within an ovarian cell. More strictly, the ovules are in pairs, as there are but three primary sections or carpels, divided by three primary divisions or dissepiments. Figure 4 shows a transverse section of one of these primary divisions or carpels which well indicates the position of the ovules (*a*), the funiculus (*b*), the placenta (*c*), and the ovarian cell (*d*). As the fruit enlarges, the three secondary dissepiments narrow and coalesce, while the other three widen, so that the pod becomes practically three-lobed and the seeds are more distinctly

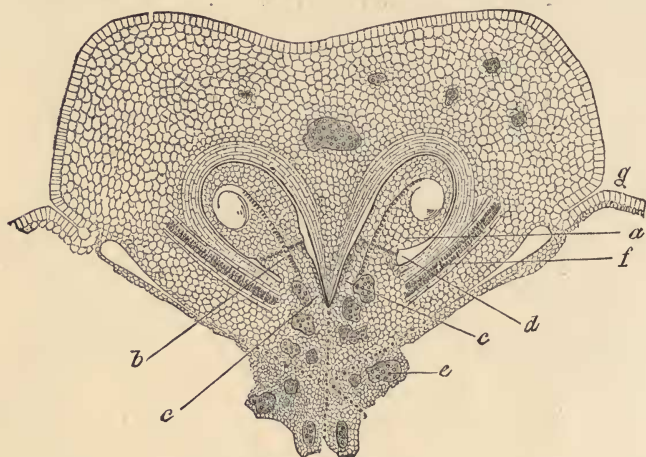


FIG. 4.—Transverse section of one of the carpels of *Yucca* pistil: *a*, ovule; *b*, funiculus; *c*, placenta; *d*, ovarian cell; *e*, fibro-vascular bundles; *f*, fibro-vascular tissue; *g*, primary dissepiment $\times 9$.

in pairs, the inner side straight and the external quite convex. In oviposition the young fruit is pierced just within the ridge in the depression occupied by the stamens, and almost always on the side of one of the primary or deeper divisions, where the walls are thinnest, so that the ovipositor enters the ovarian cell at the external or rounded side of an ovule and does not ordinarily touch the ovule itself. Rarely, however, the ovipositor penetrates the ridge and passes between two of the ovules, or sometimes even penetrates one, this last case being, however, quite exceptional.

“The egg is an extremely delicate thread-like structure, averaging 1.5 mm. in length and less than 0.1 mm. (Fig. 1, *m*, *n*, *o*)

in diameter, tapering at the base and enlarging slightly toward the capitate end, which has also a slightly indurated point. It is impossible to follow it with the unaided eye or in fact with an ordinary lens, even if the pistil be at once plucked and dissected; but by means of careful microscopic sections we may trace its course. From the position assumed by the moth, the ovipositor punctures the pistil somewhat obliquely, but as the egg is much longer than the diameter of the ovarian cell, the delicate oviduct of the moth bends and then runs vertically along the inner part of the cell next the placenta, and leaves the egg extending in this longitudinal direction along some seven or eight ovules, as shown in the illustrations (Fig. 5, *c, c*). The apical end of the

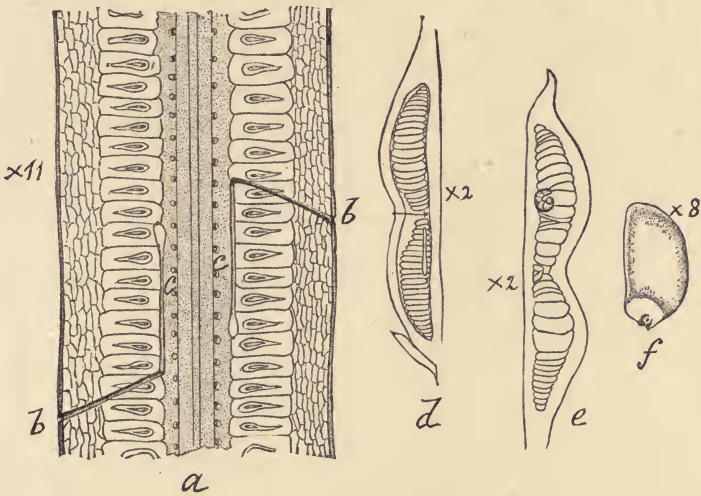


FIG. 5.—*a*, longitudinal section of pistil of *Yucca filamentosa*, showing (*b, b*) punctures of *Pronuba*, and (*c, c*) the normal position of her eggs in the ovarian cell; *d*, section of a punctured carpel 7 days after oviposition, showing the egg yet unhatched and the manner in which the ovules in the neighborhood of puncture have been arrested in development so as to cause the constriction; *e*, section of an older carpel, showing the larva above the original puncture; *f*, a seed 13 days from oviposition, showing young larva at funicular base—enlargements indicated.

egg soon enlarges (Fig. 1, *n*), and the embryo may be seen developing in it very much as in the case of the similarly elongate eggs of gall-flies (*Cynipidæ*), though the pedicel does not shorten, as observed in these last. Segmentation is noticeable on the second day, and the *Yucca* ovule at once begins to swell and enlarge, the irritation (doubtless mechanical) influencing the plant tissue much as in the case of the punctures of the gall-flies

just mentioned. Sometimes two or more adjacent ovules are thus affected."

It may be well right here to look a little more closely into the minuter characteristics of the *Yucca* flower at this stage of its development that we may understand more fully the action and influence of the moth. In my first article, published some twenty years ago, announcing the discovery of *Pronuba* and its action on *Yucca* pollination, I was strongly inclined to the idea that the act of pollination had some compensating inducement to the moth, aside from the impelling instinct of perpetuation of the species. At that time it was supposed that the stigmatic liquor was nectarian, and the conclusion was justifiable that the moth, attracted to it for feeding purposes, would incidentally induce pollination. On this view of the matter it did not require a great stretch of the imagination to conceive that the pollen might also incidentally accumulate in the spines, and that the vigorous action of the head that had been noticed might even be considered as an effort to get rid of the encumbrance while feeding. In those days I was more imbued with the common notion that lower creatures are impelled for the most part unconsciously to their acts. Twenty years of study and experience have only served to prove the acts of *Pronuba* the more unselfish and without food inducement. A longitudinal section of the upper portion of the pistil will show the style with the stigmatic tube, which at this time communicates with the ovarian cells. Now, Trelease has shown that the stigmatic liquor is not nectarian, but that the slight amount of nectar associated with the flower is secreted in pockets formed by the partitions that separate the three cells of the pistil, and which open externally near the style by a contracted pore from which the nectar is poured through a capillary tube to the base of the pistil. The accompanying illustration (Fig. 6) renders this more intelligible, *a* being a longitudinal section through the center of a pistil, showing the septal gland (*g*), the duct (*d*), and the outlet at base; *b*, a cross-section of the pistil about the middle, also showing the duct (*d*) and gland (*g*); *c*, a more enlarged cross-section of the nectar apparatus; *e* showing more fully the structure of the septal gland, while *h* is a longitudinal section of the top of the pistil, through the lobes, showing how the stigmatic tube (*s*) connects with the ovarian cell (*o c*), *o* being the ovary, *f* the funiculus, *p* the placenta, and *f v* fibro-vascular tissue.

These interesting facts, which I have fully verified, show that nectar-feeding insects seek it not about the stigma, but at the base of the stamens or of the petals, whether within or without. In short, the nectar in these *Yucca* flowers has no value in pollination, and *Pronuba*, in collecting the pollen and transferring it to the stigma, finds no food compensation, a conclusion which is confirmed by a study of the minute structure and internal

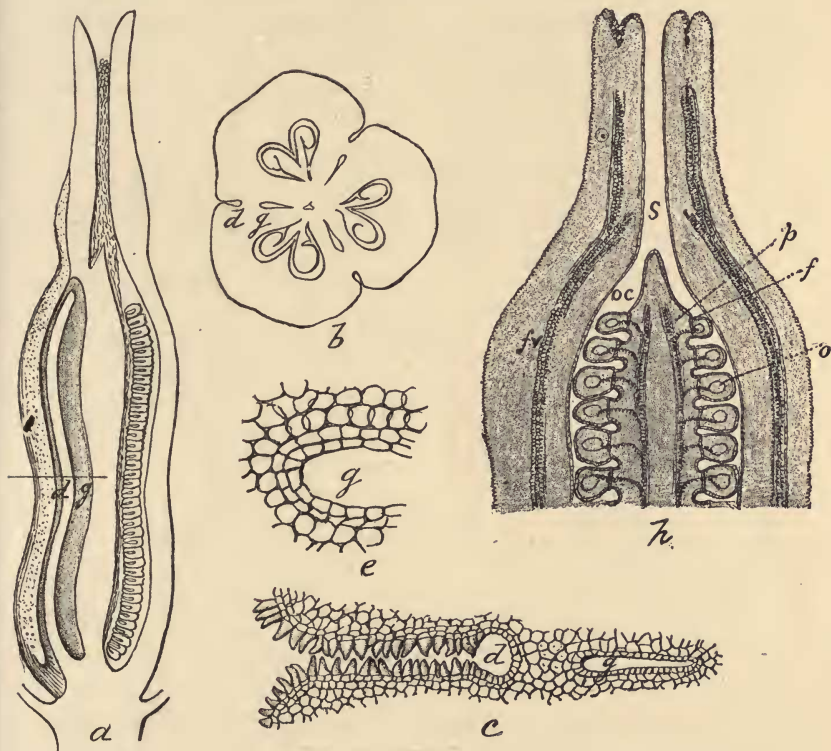


FIG. 6.—Nectar apparatus of *Yucca*: *a*, longitudinal section of pistil, with duct (*d*) and gland (*g*); *b*, cross-section about middle, showing same parts; *c*, still more enlarged cross-section of nectar apparatus; *e*, structure of septal gland—after Trelease; *h*, longitudinal section of top of pistil, showing stigmatic tube (*s*) ovarian cell (*oc*), ovule (*o*), funiculus (*f*), placenta (*p*), and fibro-vascular tissue (*fv*).

anatomy of the moth, which indicate that the tongue proper, though strongly developed, has to a great extent, if not entirely, lost its function as a sucking organ, and that the alimentary canal is practically functionless, being aborted before reaching the anus. This defunctionization, if I may use the term, of im-

portant structures has not proceeded so far in *Pronuba yuccasella* as in *P. maculata*, which pollinizes *Yucca whipplei*. Those not familiar with the structure of Lepidoptera will hardly appreciate the modifications to which I shall allude, however, without the preliminary statement that the tongue in Lepidoptera consists of two distinct parts (maxillæ) which are more or less concave on their inner side and united at the borders of the concave portion by certain locking arrangements to form between them the sucking tube. Now, while in most cases the two parts may be relaxed and separated by force, in nature they are never so separated, while the tip of the tongue is more or less acuminate and the two parts here very firmly united.

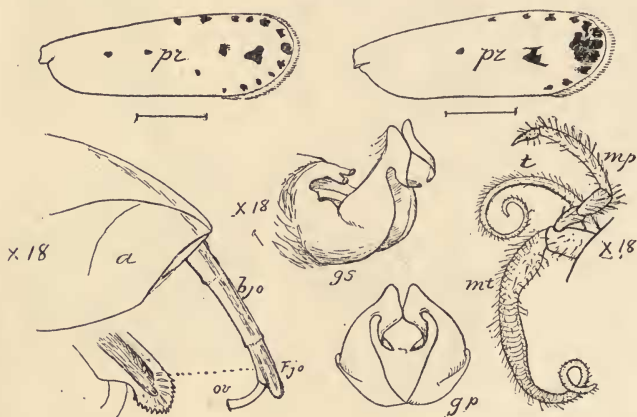


FIG. 7.—*PRONUBA MACULATA*: *a*, tip of female abdomen; *bj o*, basal joint of ovipositor; *tj o*, terminal joint of ovipositor; *ov*, oviduct; *mp*, max. palpus; *mt*, maxillary tentacle; *t*, tongue; *gs*, claspers of male from side; *gp*, claspers of male from behind—enlargement indicated; *pr*, front wings, showing arrangement of spots in two of the more common forms, hair-lines showing natural size.

In *Pronuba yuccasella* I had often noticed that the two parts became separated and in fact were almost always separated toward the tip, thus suggesting a loss of function as a sucking organ, but otherwise the tongue is strongly developed, and, with the exception of the weakness of the locking arrangement, not particularly abnormal. In *Pronuba maculata*, however (Fig. 7), the two parts of the tongue are but very feebly united, and often more or less disconnected, and are actually thickly covered with minute hairs and more sparsely with longer spinous hairs, intermixed; they are also swollen and enlarged toward the base. The import of this fact can best be conveyed to you by the statement

that in all other Lepidoptera that I know of the tongue is a smooth organ and in no way armed, except near the tip. In short, the tongue in *Pronuba maculata* has become an accessory tentacle, serving and helping in pollination, but probably incapable of use for feeding purposes. These structural peculiarities justify the conclusion, which observation confirms, that *Pronuba* does not feed in the imago state. In other words, she has no incentive to go to the stigma with her load of pollen other than that of pollinizing, and the slight amount of nectar which the plant secretes is well calculated to lead other insects which seek it away from the stigma and thus not to interfere with *Pronuba*'s mission.

DEVELOPMENT AND TRANSFORMATIONS OF PRONUBA.

On this subject I need only remark that the action of oviposition causes a disorganization of the plant tissue in the immediate neighborhood of the apical portion of the egg and the swelling of the adjacent ovules; that the embryo develops in the capitate end of the egg, and while the larva is white at first, or of the exact color of the young ovule, it becomes slightly greenish or roseate when full grown, which is in about a month, or coincident with the ripening of the seed. It perforates the capsule and drops to the ground, having six thoracic legs, which doubtless aid it at this period of its life. It remains through the fall, winter, and early spring months in a tough cocoon, transforms to the chrysalis state about a week before the *Yuccas* bloom again, and finally issues as a moth to continue the annual cycle of its career. The chrysalis (Fig. 8), has a capitate spine and a series of dorsal spines, some of which are spatulate and admirably fitted for helping it to work through the ground.

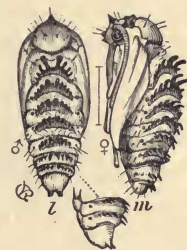


FIG. 8. — PRONUBA YUCCASELLA: *z*, male; *m*, female chrysalis.

“The effect of the puncture of the female moth on the fruit is at once noticeable by a darker green discoloration externally. In time this becomes a depression, causing a constriction of the pod, and the irregularities of the pod (Fig. 9, *b*, *c*), which have been supposed to be characteristic of the genus *Yucca*, are really due to these punctures, which ordinarily occur just below the middle.” The absolute need of *Pronuba* in the pollination of our deniscent *Yuccas* I have proved over and over again, in many

ways. The plant never produces seed where *Pronuba* does not exist; it never produces seed when she is excluded artificially, and experiments which I have made with artificial or brush pollination all show that it is much more difficult to ensure complete fructification than would at first appear, and that the act of pollination is rarely performed with a brush or by using the flower's own filaments, as successfully as it is done by *Pronuba*. It is *Pronuba yuccasella* which pollinizes all our *Yuccas* east of the Rocky Mountains, so far as known, and the species is remarkably uniform in character, its appearance in time being coëtaneous with the flowering of *Yucca filamentosa*. On the western plains its appearance has become adapted to the flower-

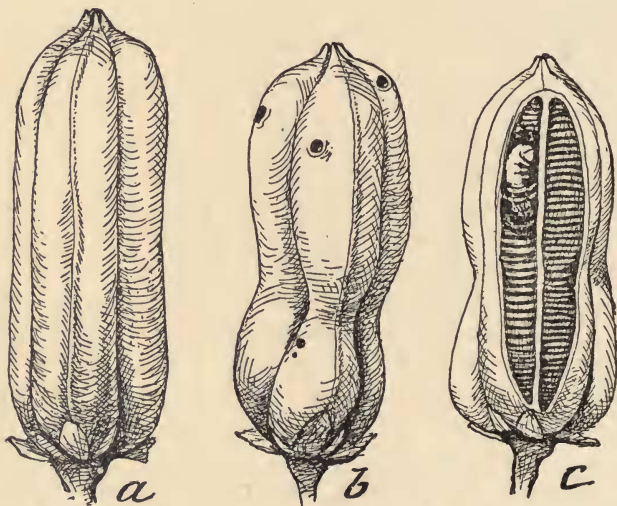


FIG. 9.—Mature pods of *Yucca angustifolia*: *a*, artificially pollinated and protected from *Pronuba*; *b*, normal pod, showing constrictions resulting from *Pronuba* puncture and exit holes of larva; *c*, one of the lobes cut open, showing larva within.

ing of *Yucca angustifolia*, but in the east, where these two species of *Yucca* are frequently grown side by side, *Y. angustifolia* flowers two or three weeks earlier than *Y. filamentosa* and generally too early to receive the visits of *Pronuba*, so that it produces seed only on very rare occasions. *Yucca brevifolia* is pollinized by *Pronuba synthetica* Riley, the most remarkable species of the genus, having very stout maxillary tentacles, a very stout ovipositor, shorter than that of *yuccasella*, but characterized chiefly by having fuliginous and unsealed wings and a polished, naked and flattened body—structures all well adapted for crawling between and about the compact and crowded flowers, with their

thick and leathery petals, but very abnormal in the Lepidoptera. In fact, this species strongly recalls in its general aspect some of the saw-flies belonging to the genus *Dolorus*, the resemblance being heightened by the rather conspicuous, cenchri-like spots, and by the conspicuous division between thorax and abdomen. It also strikingly recalls some of the Neuroptera, as *Sialis infumata*.

Now these resemblances to insects of different Orders and to families which are generally conceded to be of low type within their Order, cannot possibly be mimetic, as there can be no conceivable cause, purpose, or advantage in the mimicry. It is also impossible to account for these resemblances upon any present genetic connection. Yet we are hardly justified in disposing of them as merely accidental and without meaning. They suggest a possible synthesis in the past, when types were less specialized and present Orders had not become so well differentiated.

Yucca whipplei, which occurs in southern California, has flowers distinguished by their relatively long and stout stamens, the pollen of which is copious and glutinous, not to say mucilaginous, and a short, contracted style, with the stigma, however, expanded and covered with sticky threads. It is pollinized by *Pronuba maculata* Riley, which, as already shown, has a tongue modified into an accessory pollen-gathering organ. If any species of *Yucca* would seem not to need a special insect for pollination, *Yucca whipplei* is that species; for the long stamens, the sticky and abundant pollen, and the peltate, hairy stigma would all seem to facilitate ordinary pollination. Nevertheless, the very restricted style would seem to be purposely developed to counteract these other facilities, and we find a *Pronuba* associated with it, with a remarkably modified tongue, and with the maxillary tentacles very long and attenuated at the tip—structures which doubtless enable the moth to perform the act of pollination. I have never been able to observe the act, nor has any one yet recorded either the acts of pollination or oviposition. There will be nothing peculiar about the latter, but I shall be very glad to get actual experience in reference to the former, as I am satisfied that the observed facts will show, still more fully than in the case of *Pronuba yuccasella*, that the special modifications of both flower and insect have gone on until the mutual interdependence has become absolute.

There is much yet to learn of the pollination of other species of *Yucca*, and I am particularly anxious to obtain the insects which will doubtless be found associated with them. The regal

tree *Yucca*, *Yucca filifera*, of northeastern Mexico, reaching a height of fifty feet, with its pendulous panicles five or six feet long, has a very elongate pistil and comparatively short stamens. The few pods which I have been able to examine indicate the presence of a *Pronuba* and doubtless of a distinct species which will prove very interesting. *Yucca baccata*, *Y. treculiana*, and all the species which are sufficiently distinctive in characters and in range, may be expected to have special *Pronubas* associated with them.

THE BOGUS YUCCA MOTH.

An interesting fact connected with *Pronuba* and *Yucca* pollination is that there is always associated with *Pronuba yuccasella* another moth, which bears such a remarkable superficial resemblance to it, though possessing no power of pollination, that it

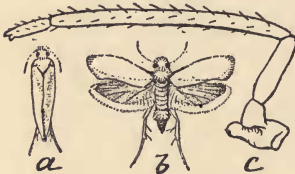


FIG. 10.—*PRODOXUS DECIPENS*: *a*, imago, wings closed; *b*, female imago, wings expanded—natural size; *c*, enlarged maxillary palpus with its basal tubercle.

has caused much confusion in the past on the part of careless observers and led to a good deal of misstatement and error. This is what I have called the Bogus Yucca Moth, *Prodoxus decipiens* (Fig. 10). In size it is somewhat smaller, on the average, than *Pronuba*, and, while found associated with it, appears rather earlier. The female has no maxillary tentacle, but otherwise the genus has all the characteristics which would place it in the same family as *Pronuba*. The ovipositor is a stronger instrument (Fig. 11), but structurally homologous. The eggs are thrust into the stem while yet tender; they are elongate in form, but short and rounded at both ends, resembling the undeveloped ova in the ovaries of *Pronuba*. The larva is absolutely apodous (Fig. 12, *a*), forms its cocoons within the stem, and transforms the ensuing year to a chrysalis, which has a much stronger capitate

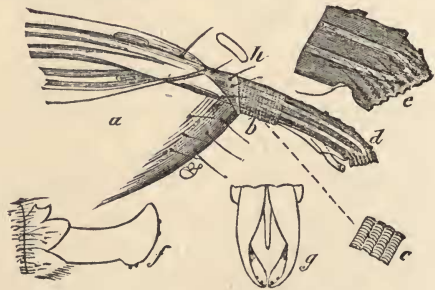


FIG. 11.—GENITAL CHARACTERS OF *PRODOXUS DECIPENS*: *a*, tip of ♀ abdomen rendered somewhat transparent; *b*, basal joint of ovipositor; *c*, its sculpture; *d*, terminal joint of same, its tip more enlarged; *e*, its sculpture; *f*, genitalia of ♂ from side; *g*, do from above; *h*, egg.

spine, but the barest trace of dorsal spines on the abdominal joints. It issues partly from the stem in giving out the moth. As I have elsewhere remarked:

“Who, studying these two species in all their characters and bearing, can fail to conclude that, notwithstanding the essential differences that distinguish them not only specifically, but generically, they are derived from one and the same ancestral form? *Pronuba*, depending for its existence upon the pollination of the flower, is profoundly modified in the female sex in adaptation to the peculiar function of pollination. *Prodoxus*, dwelling in the flesh of the fruit or in the flower-stem and only indirectly

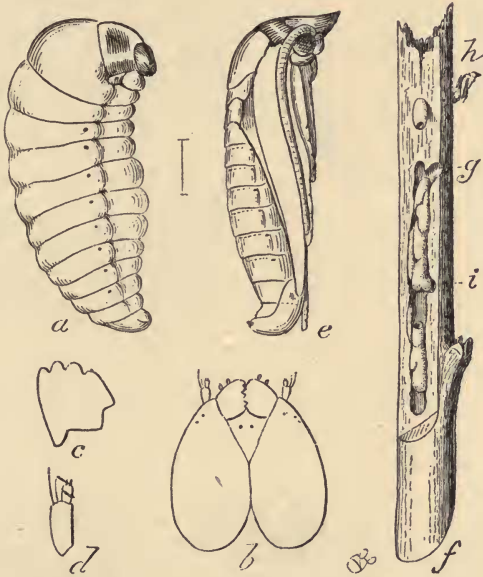


FIG. 12.—*PRODOXUS DECIPIENS*: *a*, larva; *b*, head from above; *c*, *d*, left jaw and antenna; *e*, pupa; *f*, infested stem cut open to show the burrows, castings, cocoons, and pupa shell (*h*)—all enlarged but *f*, the hair-line between *a* and *e* showing natural length.

depending upon the fructification of the plant, is not so modified, but has the ordinary characters of the family in both sexes. In the former the larva quits the capsules and burrows in the ground; it has legs to aid in its work, while the chrysalis is likewise beautifully modified to adapt it to prying through the ground and mounting to the surface. The latter, on the contrary—never quitting the stem—has no legs in the larva state, and in the chrysalis state is more particularly adapted, by the

prominence of the capital projection, to piercing the slight covering of the stem left ungnawed by the larva. The former is very regular in its appearance as a moth at the time of the flowering of the Yuccas in their native range. The latter appears earlier, as the food of its larva is earlier ready, and the female could not oviposit in the riper stem."

Some ten species of this genus *Prodoxus* have been described, all of them having the very same structural characteristics and

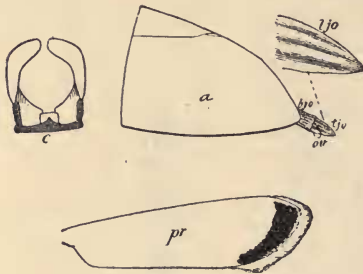


FIG. 13.—*PRODOXUS MARGINATUS*: *a*, anal abdominal joint of female — $\times 26$; *b j o*, basal joint of ovipositor; *t j o*, terminal joint do.; *ov*, oviduct; *c*, claspers of male from above — $\times 18$; *pr*, front wing—hair-line showing natural size.

in the adolescent states being scarcely distinguishable. *Prodoxus decipiens* is associated with *Pronuba yuccasella* east of the Rocky Mountains, and *Prodoxus sordidus* is similarly associated with *Pronuba synthetica*, breeding in the flower stems of *Yucca brevifolia*. All the other species are associated with *Pronuba maculata*, breeding either in the base of the capsules or in the flower stem or the main stem of *Yucca whipplei*. I have found *Prodoxus* larvæ in the stems of all other *Yuccas* which I have been able to examine, and doubtless a number of other species are yet to be discovered and characterized. The species so far known are interesting in that they illustrate in a remarkable manner what I have called fortuitous variation, or superficial colorational characters; also a great tendency to graduate into each other by variations among themselves, not only in the structure of the ovipositor and the male genitalia but in the wing markings. The time to which these remarks are limited will prevent my going into descriptive details, and

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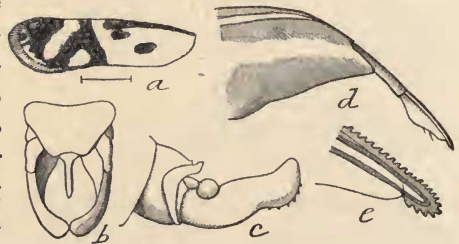


FIG. 14.—*PRODOXUS Y-INVERSUS*: *a*, left front wing, hair-line underneath showing natural size; *b*, genitalia of male, dorsal view — $\times 14$; *c*, do., lateral view — $\times 18$; *d*, anal joint of female with ovipositor exerted, lateral view — $\times 20$; *e*, tip of ovipositor still further enlarged.

I content myself with illustrating in this connection a few of the more distinctly marked species, Figs. 13, 14, 15, and 16. The genus interests us most, however, in indicating how *Pronuba* with all her abnormal, peculiarities, has been evolved; for though we have striking differences in habit and mode of development, of larva, pupa, and imago, between *Pronuba* and *Prodoxus*, yet the affinities are equally striking, and the two genera exemplify in an exceptional degree the power of natural selection to intensify habits and structures in opposing directions according to the requirements of the species. *Prodoxus* is practically dependent upon *Pronuba*.



FIG. 15.—*PRODOXUS COLORADENSIS*: *a*, left front wing, hair-line underneath showing natural size; *b*, male genitalia, dorsal view — $\times 15$; *c*, do., lateral view — $\times 18$.

for if the latter did not fructify the plant, the former would have in time no flower stems to breed in, and while *Prodoxus* has gone on, generation after generation with comparatively little change, *Pronuba* has become profoundly specialized to fit it for a more specific purpose.

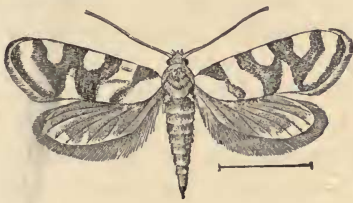


FIG. 16.—*PRODOXUS RETICULATUS*: Female with wings expanded—hair-line showing natural size.

CAPRIFICATION OF THE FIG.

It was my intention here to explain to you some interesting facts as to the caprification of the fig and the remarkable structural peculiarities and influence of the caprifig insects. It is, however, a somewhat complicated subject, and I could not within the time allotted me do justice both to it and the matter of *Yucca* pollination. As an indication, however, of how profoundly modified in this particular case the plant and the insect have become in their mutual adaptation, I may state that the perfect *Smyrna* fig, the most esteemed of the edible species, can be produced only by the intervention of the *Blastophaga psenes*, and that Dr. D. D. Cunningham has recently shown, in the *Annals of the Royal Botanical Gardens of Calcutta*, vol. I, Appendix L, 1889, by repeated examinations of the fruit of *Ficus roxburghii*, that pollination, in the ordinary meaning of that term, is, in that

particular case, out of the question, and that the development of the seed in this species is exclusively due to the stimulation of the tissues caused by the puncturing of the Blastophagas; in other words, that these insects actually represent the male element in the fertilization. This is certainly the most extraordinary phenomenon in the history of fertilization, and if confirmed—and Dr. Cunningham has been most careful and circumspect in his work—it will give a more striking instance than any we have hitherto obtained of the mutual interdependence which plants and insects may attain and the surprising manner in which they may modify each other.

GENERALIZATION.

The peculiarities which I have endeavored to present to you are full of suggestion, particularly for those who are in the habit of looking beyond the mere facts of observation in endeavors to find some rational explanation of them; who, in other words, see in everything they observe significances and harmonies not generally understood. The facts indicate clearly, it seems to me, how the peculiar structures of the female *Pronuba* have been evolved by gradual adaptation to the particular functions which we now find her performing. With the growing adaptation to *Pronuba's* help, the *Yucca* flower has lost, to a great extent, the activity of its septal glands; yet coincident with it we find an increase in the secreting power of the stigma. This increase of the stigmatic fluid has undoubtedly had much to do with originally attracting the moth thereto, while the pollinizing instinct doubtless became more and more fixed in proportion as the insect lost the power or desire of feeding. With the mind's eye I can look back into the past and picture the gradual steps by which the *Prodoxids* to which I have alluded have differentiated along lines which have resulted in their present characteristics. On the one side I see variations which have become sufficiently fixed to be considered specific; yet which can have no especial bearing on the life necessities of the species, but are a consequence rather of that universal tendency to variation with which every student of Nature becomes profoundly impressed. Thus the wing-markings vary from a darker general coloring, as in *Prodoxus ænescens*, to a more uniform intermixture of the black scales among the white, as in *cinereus*, or a sparser intermixture thereof, as in *pulverulentus*. The disposition of the black scales is in spots or bands, whether transverse or longitudinal, as in *marginatus*, *reticulatus*,

Y-inversus, etc. These are fortuitous variations, for I cannot believe that the disposition of these marks where, as in these cases, they take every form that is conceivable, can be of any benefit to the species, any more than the mere variation in the number of lobes in the leaves of different oaks growing under like conditions can be of any particular benefit to the species, however useful to us in classification.

In my address before the Section of Biology of the American Association for the Advancement of Science, at Cleveland, in 1888, I have discussed the various forms and causes of variation, and especially the limitations of natural selection, stating expressly that this last "deals only with variations useful to the organism in its struggle for existence, and can exert no power in fixing the endless number of what, from present knowledge, we are obliged to consider fortuitous characters," and I have long recognized, from my studies of insect life, the existence of these fortuitous variations. The subject has since been very well elaborated by Professor Ward in his communication to the Society (December 15, 1888) on "Fortuitous variation as illustrated by the genus *Eupatorium*" and in his Annual Address (January 24, 1891) on "Neo-Darwinism and Neo-Lamarckism," and the *Prodoxidæ* furnish an excellent illustration of this fortuitous variation. Yet at the same time that we note this chance variation, as exemplified in a number of the species of *Prodoxus*; which are mere ravagers or despoilers and have not been brought into any special or mutual relations with the plant, we have, on the other hand, in *Pronuba yuccaseila*, correlated with the other striking structural modifications which have brought it into such special relations with the plant, an elimination of all maculation or markings upon the primaries, and a purely white coloring so fixed that it shows absolutely no variation over half the continent. The structural variation has been necessary—a consequence of effort, environment, and natural selection. The color variation, on the contrary, has not been absolutely necessary, yet has nevertheless gone on in lines which, tending to give greater protective resemblance to the flower, have in the long run proved to be, perhaps, the most advantageous. I thus recognize three distinct lines of variation as exemplified in these *Prodoxidæ*, and what is true of them is, I believe, true of all alliances of organisms. The first and most important is structural and generic; it is absolutely essential and is preserved in its perfection by the elimination, through

natural selection, of all forms departing from it. The second is merely coincident, not essential, but nevertheless along lines that are of secondary advantage. The third is purely fortuitous, affects superficial features in the main, is unessential (a consequence of the inherent tendency of all things to vary), and takes place along all lines and in all directions where there is no counteracting resistance.

Now, when it comes to the bearing which the history of these little moths has upon some of the larger questions that are now concerning naturalists (for instance, the transmission of acquired characters, or the origin, development, and nature of the intelligence displayed by the lower animals), broad fields of interesting opinion and conclusion open up before us—fields that cannot possibly be explored without trenching too much upon your time. I will close, therefore, with a few summary expressions of individual opinion, without attempting to elaborate the reasons in detail, and with the object of eliciting further discussion, which is one of the objects of the paper. My first conviction is that insect life and development give no countenance to the Weismann school, which denies the transmission of functionally acquired characters, but that, on the contrary, they furnish the strongest refutation of the views urged by Weismann and his followers. The little moths of which I have been speaking, and indeed the great majority of insects—all, in fact, except the truly social species—perform their humble parts in the economy of nature without teaching or example, for they are, for the most part, born orphans, and without relatives having experience to communicate. The progeny of each year begins its independent cycle anew. Yet every individual performs more or less perfectly its allotted part, as did its ancestors for generation after generation. The correct view of the matter, and one which completely refutes the more common idea of the fixity of instinct, is that a certain number of individuals are, in point of fact, constantly departing from the lines of action and variation most useful to the species, and that these are the individuals which fail to perpetuate their kind and become eliminated through the general law of natural selection.

Whether these actions be purely unconscious and automatic or more or less intelligent and conscious does not alter the fact that they are necessarily inherited. The habits and qualities that have been acquired by the individuals of each generation could have become fixed in no other way than through

heredity. Many of these acts, which older naturalists explained by that evasive word "instinctive," may be the mere unconscious outcome of organization, comparable to vegetative growth; but insects exhibit all degrees of intelligence in their habits and actions, and they perform acts which, however voluntary and, as I believe, conscious in many cases, as in that of our Yucca Moth, could not be performed were the tendency not inherited. Every larva which spins or constructs a hibernaculum, or a cocoon in which to undergo its transformations, exemplifies the potent power of heredity in transmitting acquired peculiarities. A hundred species of parasitic larvæ, *e. g.*, of the family Braconidæ, which in themselves are almost or quite indistinguishable from one another structurally, will nevertheless construct a hundred distinctive cocoons—differing in form, in texture, in color, and in marking—each characteristic of its own species and in many instances showing remarkable architectural peculiarities. These are purely mechanical structures, and can have little or nothing to do with the mere organization or form or structure of the larva, but they illustrate in the most convincing manner the fact that the tendency to construct and the power to construct the cocoon after some definite plan must be fixed by heredity, since there is no other way of accounting for it. This fact alone, which no one seems to have thought of in the discussion, should be sufficient to confound the advocates of the non-transmissibility of acquired characteristics.

Thus to my view modification has gone on in the past, as it is going on at the present time, primarily through heredity in the insect world. I recognize the physical influence of environment; I recognize the effect of the interrelation of organisms; I recognize, even to a degree that few others do, the psychic influence, especially in higher organisms—the power of mind, will, effort, or the action of the individual as contradistinguished from the action of the environment; I recognize the influence of natural selection, properly limited; but above all, as making effective and as fixing and accumulating the various modifications due to these or whatever other influences, I recognize the power of heredity, without which only the first of the influences mentioned can be permanently operative.

Let us stop for a moment to ponder what the intricate adjustments between plants and animals, and especially between plants and insects, mean, when these have become so profoundly modified by each other that their present existence actually de-

pends the one on the other. As palæontology shows, and as Professor Ward has more particularly so well explained, there was for ages no vegetation but the flowerless plants. The first were the low cellular cryptogams, consisting chiefly of marine algæ, and these, the lowest and first organisms upon the planet, have endured through all geologic time and obtain to-day. Next, beginning in the upper Silurian and reaching their maximum in the Carboniferous, came the vascular cryptogams, of which the ferns constituted the bulk. Arborescent and gigantic compared with present forms, they mingled with the now extinct Lycopodineæ to form the bulk of the forests of the coal period. Then came the Phanogams, or flowering plants, and in this great division the Cycadaceæ and coniferæ (pines, firs, etc.) were the chief forms during Mesozoic times. So far the seed has been exposed. Now come the Angiosperms, in which the seed is protected in the ovary or pericarp, and the Monocotyledons (palms, sedges, etc.) precede the Dicotyledons, while of these last the Apetalæ, Polypetalæ, and Gamopetalæ succeed each other in the order of their naming.

In brief, to use his own words, the development has been from the simple to the complex; from the flowerless to the flowering; from the endogenous to the exogenous; from the apetalous to the gamopetalous; and this succession corresponds to the best systems of classification of existing forms.

Both Cryptogams and Phanogams began existence during the Silurian, and there has been a race for supremacy ever since, with our present flora as the result. It is also a fact of the greatest significance that the same palæontological evidence which gives us this record also tells us that there has been a corresponding development of insect life, from the lower Neuroptera and Orthoptera, which prevailed in the days when Anemophilous plants reigned, to the higher Lepidoptera and Hymenoptera, which appeared only as the higher flowering plants developed in the Jurassic and Cretaceous.

I do not hesitate, in this connection, to refer to another of Professor Ward's conclusions set forth in one of his interesting articles, namely, that most of the higher flowering plants would speedily perish were insect aid withdrawn, and that but for such aid in the past we should now be without most of our gorgeous flora, and that insects have actually paved the way for man's existence by the part they have played in the development of fruit and nut bearing plants.